Length-weight relationships of mesopelagic fishes from the equatorial and tropical Atlantic waters: influence of environment and body shape

Cristina López-Pérez[1], M. Pilar Olivar[1], P. Alexander Hulley[2,3], Víctor M. Tuset[1]

[1]Instituto de Ciencias del Mar (CSIC), Passeig Marítim 37-49, Barcelona 08003, Spain,

[2]Iziko – South African Museum, Cape Town, South Africa

[3]MA-RE Institute, University of Cape Town, South Africa

Correspondence:

Víctor Manuel Tuset Andújar, Instituto de Ciencias del Mar (CSIC), Passeig Marítim 37-49, Barcelona 08003, Spain.

Email: vtuset@icm.csic.es

Abstract

Length-weight relationships (LWR) were estimated for 36 mesopelagic fish species collected from the equatorial and tropical Atlantic encompassing several oceanographic regions: oligotrophic, equatorial, Cape Blanc, Cape Verde and the Canary Islands. The sample was composed of myctophids (25 specimens), gonostomatids (5), sternoptychids (3), stomiids (2) and phosichthyids (1). The species were clustered according to body shape: 'short and deep' (sternoptychids), 'elongate' (gonostomids, stomiids and some phosichthyids) and 'fusiform' (myctophids and some phosichthyids). Three types of weight and LWRs were considered: wet weight (*WW*), eviscerated wet weight (*eWW*) and eviscerated dry weight (*eDW*). The study demonstrated that most species present a positive allometric growth, independent of the weigh used. However, the allometric value varied in 40-50% of species depending on the type of weight considered. Significant variations linked to fish morphology were found in the relationship between the slope and intercept of the LWR equation. Significant differences were also noted in the water content linked to fish body shape. Based on the distributions of several species we compare their fitness between oceanographic regions using the relative condition factor (K_{rel}). Except for *Diaphus brachycephalus* (oligotrophic *vs* equatorial waters) and *Lampanyctus alatus* (equatorial, Cape Blanc, Cape Verde and the Canary Islands), no regional significant differences were observed in the species analysed**.**

KEYWORDS

mesopelagic fishes, oceanographic gradient, morphology, size-weight growth, Atlantic Ocean

1. INTRODUCTION

Mesopelagic fishes have a worldwide distribution from the Arctic to the Antarctic (Krefft, 1974; Hulley, 1981), although species richness and annual production are commonly greater in subtropical and tropical regions (Gjøsaeter & Kawaguchi, 1980). They are generally small to medium-size fishes, including a high diversity of species, numerically dominated by bristlemouths (family Gonostomatidae) and other Stomiiformes, and by lanternfishes (Order Myctophiformes), the majority of which live in the ocean's twilight zone (by definition between 200 and 1000 m). Some, particularly myctophids, undertake diel vertical migrations following their prey into the epipelagic zone to feed at night (Sutton *et al*., 2008, 2013; Davison *et al*., 2013; Bernal *et al*., 2015; Choy *et al*., 2015; Wang *et al*., 2019). During daytime, and mainly to avoid predators, they descend into deeper waters mainly to avoid predators where they undertake digestion and excretion. This results in a substantial contribution to total vertical carbon flux from the surface to the deep ocean (Ikeda *et al*., 2008; Davison *et al*., 2013; Hudson *et al*., 2014; Draze and Sutton, 2017). Thus, these fishes play a key role in food web interactions linking primary consumers (e.g., copepods and macro-zooplankton) with both pelagic and deep-sea fish species, as well as other marine species such as marine mammals and birds (Springer *et al.,*1999; Pereira *et al.,* 2011; Smith *et al*., 2011; Trueman *et al*., 2014). The high species richness of stomiiform and myctophiform fishes has contributed to the lack of more detailed information on the basic aspects of fish biology, including length-weight relationships (LWR) and condition factors at the species level (Fock & Ehrich, 2010; Battaglia *et al*., 2010, 2015; Jiang *et al*., 2017; Fock & Czudaj, 2018; Wang *et al*., 2018).

LWR's have been used extensively to gather information on growth, ontogenetic changes, population dynamics and in trophic ecology studies to reconstruct and estimate the biomass of partially digested prey (Pauly, 1993; Verdiell-Cubedo *et al*., 2006; Battaglia *et al*., 2010, 2016).

In general, the parameters for LWRs differ among species due to multiple factors, including the fish body shape (Schneider *et al*., 2000; Kulbicki *et al*., 2005; Froese, 2006; Jellyman *et al*., 2013), whilst intra-specific differences may be due to gonad maturity, gender, diet, stomach fullness, health, preservation techniques, season and habitat (Beyer, 1987; Sakuma *et al*., 1999). Even, the sampling protocols (e.g., fresh, frozen or preserved in solution) can lead to variations in LWR estimations (Eduardo *et al*., 2019). Some applications of LWRs include the ecosystem-modelling approach to obtain confident production-over-biomass estimates (Christensen & Pauly, 1992; Pauly *et al*., 2000; Christensen & Walters, 2004; Torres *et al*., 2012). In this sense, LWR's from similar species and different regions are commonly used for the biomass estimation of mesopelagic fish species from acoustics (Fock & Ehrich, 2010; Fock & Czudaj, 2018), despite possible differences in allometric relationships (Atkinson, 1989). Similarly, the condition factor is considered as a proxy of fitness in determining the population health and variability of individuals and populations (Millar & Hickling, 1990; Lloret *et al*., 2002, 2014; Pazianoto *et al*., 2016; Brosset *et al*., 2018). But there is a lack of information for mesopelagic fishes (Watanabe & Kawaguchi, 2003).

The subtropical western Atlantic Ocean is one of the most oligotrophic regions of the global ocean (Morel *et al*., 2010), whereas the eastern central Atlantic is one of the four most productive regions of the world, due to upwelling (Mittelstaedt, 1983). The ocean between these two regions is characterized by the convergence of water masses originating in both the southern and northern hemispheres, and results in a complex oceanic current system (Stramma & Schott, 1999). Moreover, south of the Cape Verde archipelago, the mesopelagic layers are characterized by the presence of an oxygen minimum zone (OMZ), with dissolved oxygen concentrations corresponding to intermediate hypoxia values (Ekau *et al*., 2010; Moffitt *et al*., 2014; Olivar *et al*., 2017). Previous investigations in the area have shown that some mesopelagic fishes are associated with particular waters masses, while others occur across the entire region (Olivar *et al*., 2017, 2018). These differences in the oceanographic features may also have an influence on the trophic transfer efficiencies from plankton to fishes, which can be indirectly evaluated from body condition (Le Cren, 1951; Simpkins & Hubert, 2000; Stevenson & Woods 2006; Wilson & Nussey, 2010).

This study attempts: (i) to provide information on LWR's of 36 mesopelagic fish species collected in the tropical and equatorial Atlantic waters by using different weight variables, so as to facilitate effective use by scientists working on mesopelagic biomass estimation; (ii) to assess the changes in the fish health between oceanographic regions using the Relative Condition Factor (Le Cren, 1951); and (iii) to evaluate how the body shape influences the *a* and *b* parameters of LWR equation, as well as the water content of species. These types of information can provide useful evidence to improve the understanding of how species and individuals are structured in open waters.

2. MATERIAL AND METHODS

2.1. Sample collection

Specimens were collected during a cruise carried out in April 2015 across the equatorial and tropical Atlantic, from near the Brazilian coast (13°S 38.3°W) to south Canary Islands (28°N 15.6°E), on board R/V Hespérides. A total of 12 stations were occupied both day and night, and fish samples were obtained in different strata of the water column, from 800 m to the surface (Olivar *et al*., 2017). Ship speed was 2 knots (1 m/s) and haul duration at each strata ranged from 10 to 30 min. The sampling gear deployed was a pelagic midwater trawl, the "Mesopelagos" net (35-m² mouth opening; total length 58 m, with graded-mesh netting from 30 mm at mouth to 4 mm towards the cod end) (more details in Olivar *et al*., 2017).

The fresh samples were analysed on board. Fishes were identified to the lowest possible taxon and keep frozen at -20°C until transference to the laboratory, where their identifications were checked, and individual measurements of length and weight were taken. Standard length (*SL*) was recorded to the nearest 1 mm, using digital calipers, and whole body wet weight (*WW*) to the nearest 0.0001 g, using a digital balance. Individuals were then dissected, the digestive tract, stomach and gonads were removed, and the eviscerated wet weight (*eWW*) of each specimen was taken. To eliminate water content, eviscerated specimens were freeze-dried in a Telstar LyoAlfa 6 freeze dryer for 24 h, and the eviscerated dry weight of each specimen was then recorded (*eDW*). Water content was calculated as the difference between *eWW* and *eDW*, expressed as % *eWW*, to highlight their effect on the estimation of LWRs.

2.2. Length-weight relationships

Size and weight data were fitted using a power function: $y = \mathrm{a}x^{b}$, where x is *SL* and y the weight parameter (*WW*, *eWW* or *eDW*). The slope, b, is the allometric growth factor and the intercept, a, is the expected value of y at $x= 1$ (Gould, 1966). Data from the logarithmically transformed equations were then adjusted by the method of least squares. The values of b, their 95% confidence intervals (95% CI), and the coefficient of determination (r^2) were calculated according to the methods of Sokal & Rohlf (1979). In addition, a Student's-*t*-test was used to evaluate the isometric growth ($b= 3$), and whether b value is significantly higher or lower indicating a positive or negative allometry, respectively (Gould, 1966; Margalef, 1974; Pauly, 1984).

To assess the influence of body morphology on the intercept (a) and slope (b) parameters of the LWR (using *eDW*), a linear regression was estimated for three groups of fishes defined on the basis of their general body forms: 'short and deep' (Sternopthychidae), 'elongate'

(Gonostomatidae and Stomiidae) and 'fusiform' (Phosichthyidae and Myctophiidae). Statistical differences between the slopes were tested using an ANCOVA analysis. In addition, the average water content of each fish group was compared using a Kruskal-Wallis test (non-parametric test).

2.3. Relative condition factor

The fish condition was estimated using the Relative Condition Factor ($K_{rel} = (W_o/aSL^b$; Le Cren, 1951), which relates the observed body weight ($W_o = eDW$) of a given individual with the predicted by the length–weight relationship (aSL^b). The parameters a and b were obtained from the regional LWR derived by pooling data for all regions for each species separately (Efitre *et al*., 2009). Calculation of Fulton's Condition Index ($Kn = 100W/L^3$; Fulton, 1911) was omitted because the growth of mesopelagic fishes was not isometric (see results). The Relative Weight index (Wege & Anderson, 1978; Froese, 2006) was not used because there are no studies based on this index supporting a population differentiation of mesopelagic fishes in open ocean.

In order to perform the regional comparisons in the K_{rel}, regions of the study area were defined according to oceanographic parameters described in Olivar *et al*. (2017): oligotrophic (stations #1-3), equatorial (stations #4-6), Cape Verde islands (stations #7-10), Cape Blanc upwelling (station#11), Canary Islands (station#12) (Figure 1). For these comparisons, only 9 species (*Chauliodus danae*, *Ceratoscopelus warmingii*, *Diaphus brachycephalus*, *Diaphus mollis*, *Diaphus rafinesquii*, *Lampanyctus alatus*, *Lepidophanes guentheri*, *Myctophum nitidulum* and *Vinciguerria nimbaria*) were considered to have a sufficient number of individuals ($n > 10$) by region and LWRs with high correlations ($r^2 > 0.90$). The normality and homogeneity of variances in the K_{rel} data were checked for each species by region using the Shapiro-Wilk's test and Bartlett's test, respectively. Depending on the Gaussian distribution of data, variations of K_{rel} between two regions were compared by the Student's *t*-test (parametric test), or the Mann–Whitney's *U* Test (non-parametric test). To analyse more than two regions, a Kruskal-Wallis test followed by *a posteriori* Dunn test was performed with the package *dunn.test* v.1.3.5. in R (Dino, 2017).

All statistical analyses and graphical representations were conducted with the software R (R Core Team, 2016).

3. RESULTS

A total 1277 individuals belonging to 36 species from 5 families were analysed. The family Myctophidae was represented by 11 genera and 25 species, followed by Gonostomatidae, with 2 genera and 5 species; Sternoptychidae, with 3 genera and 3 species; Stomiidae, with 2 genera and 2 species, and Phosichthyidae, with 1 genus and 1 species (Table 1).

The determination coefficients (r^2) of the fitted equations were generally high (mean value of 0.991 ± 0.001), ranging from 0.613 for *Cyclothone pseudopallida* (Gonostomatidae) to 0.997 for *Bolinichthys photothorax* (Myctophidae). Excluding the extreme case presented by *C. pseudopallida,* 77% of the relationship have $r^2 > 0.950$ (Table 2 for *eDW*; Table S1 for *WW* and Table S2 for *eWW*, Supplementary material).

In terms of growth, the LWRs for *WW* revealed that 57.2% of the species showed isometric growth, the 30.5% positive allometry ($b > 3$) and the 11.1% negative allometry ($b < 3$). A similar tendency was also detected when fitting *eWW* (52.7%, 33.3% and 13.8%, respectively). The main differences in growth patterns between the LWRs for *WW* or *eWW* were observed for *Vinciguerria nimbaria* (Phosichthyidae), which presented a higher *b* when fitting total weight, and for *Lepidophanes guentheri* (Myctophidae) and *Sternoptyx diaphana* (Sternoptychidae) with lower *b* using eviscerated data. By contrast, LWRs for *eDW* showed a slight increment in the proportion of species with positive allometry (47.2% isometric, and 38.8% and 13.8%, positive and negative allometry, respectively). Irrespective of the fitted data, the lowest allometric coefficients were always found for *Cyclothone* spp., together with the myctophid *Diaphus vanhoeffeni*. The highest allometric growth coefficient was always in *Polyipnus polli*, and in myctophids such as *Benthosema glaciale, Ceratoscopelus warmingii, Diaphus brachycephalus, D. holti, D. metopoclampus, D rafinesquii, Lampanyctus alatus, L. pusillus, Lepidophanes guentheri, Lobianchia dofleini, Myctophum affine, M. nitidulum,* and *M. punctatum* (Table 2 for *eDW*; Table S1 for *WW* and Table S2 for *eWW*, Supplementary material). The 30.5% species showed an allometric coefficient higher for LWRs fitting with *eDW* in comparison with *WW*, and 27.8% in relation to *eWW*. Nevertheless, 52.8% and 59.3% of cases provided similar *b* values (± 0.1). In general, the greatest differences between the growth patterns were observed for 6 myctophids: *Lampanyctus pusillus*, *L. alatus*, *Diaphus metopoclampus*, *Benthosema glaciale*, *Ceratoscopelus warmingii* and *Diaphus holti*; and for the gonostomatid *Cyclothone pesudopallida*. In these cases, the higher growth rates (*b*) of the RLWs were estimated for *eDW*. In contrast, a negative difference between *b* values was noted for: *Sigmops elongatus* (Gonostomatidae), *Notolychnus valdiviae* (Myctophidae), *Argyropelecus sladeni* (Sternoptychidae), and *Chauliodus danae* (Stomiidae). Strong correlations were found between the values of *b* and log *a*, varying significantly between fish body shapes ($F_{2,32}$ = 3.486, P= 0.044, Figure 2). The slope was larger in elongated shapes (b = -1.878) and smaller in short and compressed fishes as sternoptychids (b = -1.056).

Intra-specific differences between growth patterns within species were higher when comparing *eWW* and *eDW* than between *WW* and *eWW*, which revealed the important contribution of water content. The species with higher water content (> 80%) were *Cyclothone pallida, C. acclinidens, Lampanyctus nobilis, Chauliodus danae, Sigmops elongatus* and

Stomias boa boa (Table 3). By contrast, *Notolychnus valdiviae*, *Polyipnus polli, Lampanyctus pusillus, Benthosema glaciale* and *Diaphus fragilis* had values lower than 75% (Table 3). The elongated shaped fishes were characterized by higher water content (mean and standard deviation, 81.50 ± 1.85) than fusiform fishes (76.41 ± 4.11), and the short and deep shaped species (75.99 ± 4.06). A high variability was found between groups (Kruskal-Wallis test, χ^2 = 12.81, df = 3, P = 0.002).

The mesopelagic fishes showed similar average values of K_{rel} ranging between 0.792 (*Diaphus brachycephalus* from the oligotrophic region) and 1.120 (*D. rafinesquii* from the Cape Blanc upwelling region). Regional associations in the average values of K_{rel} were found for *D. brachycephalus* (*t*-test, t = 8.817, df = 84, P < 0.0001) with lower values (0.792 ± 0.185) in oligotrophic waters than in equatorial region (0.902 ± 0.076) (Table 4), and in *Lampanyctus alatus* (Kruskal-Wallis test, χ^2 = 17.309, df = 3, P = 0), showing an increase of average K_{rel} for regions closer to African coast. The equatorial region differed from the Cape Blanc upwelling region and Canary Islands, but it was not dissimilar to Cape Verde Islands region. The K_{rel} value of Cape Verde Islands only presented differences with the average of the Canary Islands; and the Cape Blanc upwelling region and Canary Islands also reached similar average of condition (Table 4).

4. DISCUSSION

The present study contributes to knowledge of mesopelagic fishes by reporting on LWR equations for 36 species, thereby establishing the effect of different weights in the allometry of LWR's, and by comparing the environmental effect in the relative condition factor. In general, our findings seem to reinforce the theory that the growth pattern is a feature identifying each species (Mayrat, 1970) since 24 of the 36 of mesopelagic fishes analysed demonstrated similar allometric relationships, independent of the weight measure used. Some species reached a higher *b* value when fitting *WW* instead of *eWW,* reflecting the influence of full guts and, to a lesser extent, gonadal mass (e.g., *Vinciguerria nimbaria Chauliodus danae* and *Cyclothone livida*), but in other species showed the opposite effect (e.g., *Lobianchia dofleini*, *Lepidophanes guentheri* and *Diaphus vanhoeffeni*). Nevertheless, the use of eviscerated dry weight is always recommended for LWR's, since it more accurately reflects better the muscular growth, irrespective of the trophic behaviour (full or empty guts) or the gonadal weight (important at maturation) (Pauly 1984; Froese, 2006). In other instances, such as for reconstruction and estimation of biomass of partially digested prey in studies of trophic ecology, information on WW would also be relevant. Allometric coefficients (*b* for *eDW*) in the present study were within the expected range (2.5-3.5) for fishes (Froese, 2006), mostly ranging between 2.952 (25% percentile) and 3.384 (75% percentile). The most atypical allometric coefficient was observed for the myctophid *Lampanyctus pusillus,* 4.247, which could be due to the small size range analysed.

The species and sizes ranges of myctophids and hatchetfishes studied here showed a positive allometric growth, which implies a faster growth in body mass than in body length, i.e., more robust body and with a greater amount of muscle mass. This feature may help in the daily feeding vertical migrations, to the surface in myctophids and to the shallower mesopelagic depths in hatchetfishes (Olivar *et al*., 2012, 2016, 2017). The opposite pattern with negative allometric growths, i.e., faster growth in length than in weight, was mostly observed in stomiiform species such as *Chauliodus danae*, *Cyclothone acclinidens*, *C. livida*, *C. pallida* and *Sigmops elongatus*, which live in deeper waters, and which have an elongate shape and higher water content. This finding is in accordance with previous studies showing an association between the proportion of water content and distribution depth of these fishes (Childres &

Nygaard, 1973; Neighbors & Nafpaktitis, 1982; Bailey & Robison, 1986; Stickney & Torres, 1989; Pakhomov *et al*., 1996), and is also accompanied by a decrease in skeletal ash content (see Childres & Nygaard, 1973). The main reason of this somatic growth is probably due to absence of extensive vertical migrations in most of these species (Badcock and Merret, 1976; Olivar *et al*., 2017). In general, the allometric pattern found in our species did not differ from those in other studies, although slight variations can be due to exogenous and endogenous factors (e.g., Kimmerer *et al*., 2005; Jobling, 2008; Mazumder et al., 2016), as well as the type of length measurement (standard or total), and size-range analysed. For instance, Fock & Ehrich (2010) gave a wide list of LWR's for mesopelagic fishes from the North Atlantic. Their estimation of allometric coefficients were smaller than in our study (for *eDW*) for those species differing in the size range, for example in *B. glaciale* (3.647 *vs* 3.020), *D. dumerilli* (3.076 *vs* 3.018), *D. metopoclampus* (3.684 *vs* 3.074), *L. dofleini* (3.448 *vs* 2.609) and *N. bolini* (3.212 *vs* 2.331). However, they were similar when the size ranges were similar as for example in *D. holti* (3.356 *vs* 3.350), *M. punctatum* (3.363 *vs* 3.448) and *S. boa boa* (3.081 *vs* 3.184). For fishes with similar fish size-ranges, our allometric patterns were larger than in other geographical areas, for example in the Mediterranean Sea for *Diaphus holti* (3.356 *vs* 3.102) and *Lampanyctus pusillus* (4.247 *vs* 2.296) (Battaglia *et al*., 2010), and in the North-western Pacific Ocean for *Ceratoscopelus warmingii* (3.537 *vs* 3.153) (Wang *et al*., 2018).

Food availability and physical factors have a strong influence on the growth and condition factors (Le Cren, 1951). Olivar *et al*. (2017) found higher environmental gradients in terms of temperature (22ºC of difference) and salinity (3 PSU) between the sea surface and deep waters in the subtropical western Atlantic Ocean than eastern zone (10°C and 1 PSU, respectively). Although this environmental variation may affect the energetic balance and growth of specimens, any difference was detected in most species, except for *Lampanyctus alatus*. The most probable reason for the increase of the K_{rel} along the Atlantic transect may be related to the visual system, a more generalist pattern being characterized by a major visual field favouring the detection of preys in all directions (de Buserrolles *et al*., 2014, de Buserrolles & Marshall, 2107), and which is more numerous in the western sector. Finally, low values of K_{rel} (< 1) for some species (e.g., *Chauliodus danae*, *Diaphus brachycephalus*, *D. mollis* and *Vingiguerria. nimbaria*) were noted in all regions, which suggests two hypotheses: a) the energetic cost of diel vertical migration (DVM) may be higher in these species; or b) the energetic requirement may be less. Unfortunately, information on the food conversion efficiency on fish growth is not available for many mesopelagic fish species. However, the intraspecific and regional variability found in our study reinforces the importance of investigations into ecological and energetic demands of deep-sea organisms (Siebel & Drazen, 2007; Irigoien *et al*., 2014; Belcher *et al*., 2019).

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Contributions

MPO and PAH were responsible for the species identifications; CLP, conceived the initial idea and wrote the main paper in collaboration with the other co-authors; CLP, MPO and VTA conducted the statistical analysis. All authors discussed results and implications, providing significant inputs to the manuscript at all stages.

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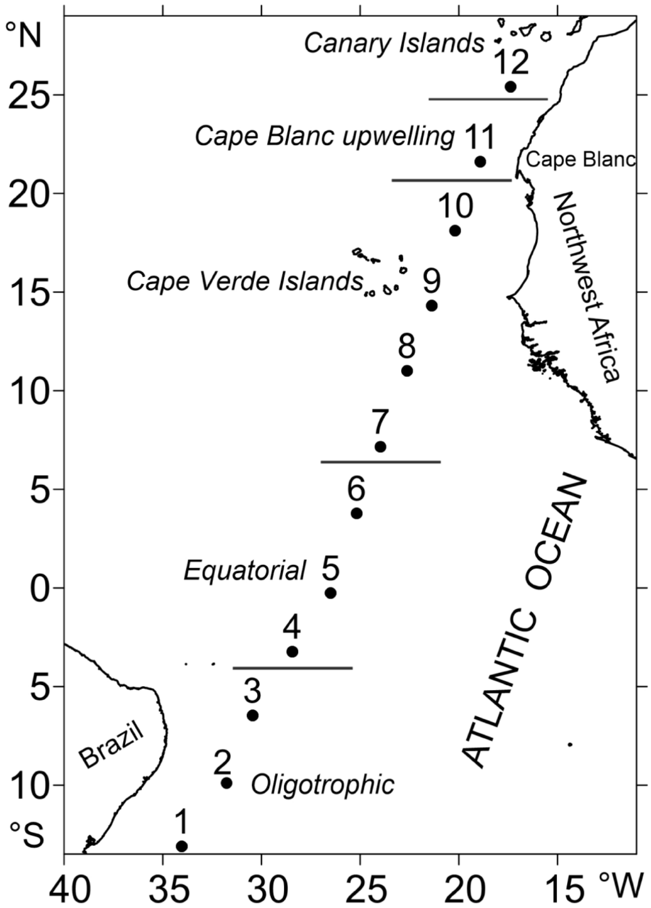
Legends

FIGURE 1 Location of the stations sampled during the survey across the equatorial and tropical Atlantic during April 2015, and oceanographic regions according to Olivar *et al*. (2017).

FIGURE 2 Relationships between the regression coefficients log *a* and *b* of LWR equation for different body shapes (short-deep, elongate and fusiform) at the species level.



°N
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Canary Islands
12
Cape Blanc upwelling
11
Cape Blanc
10
Northwest Africa
Cape Verde Islands
9
8
7
6
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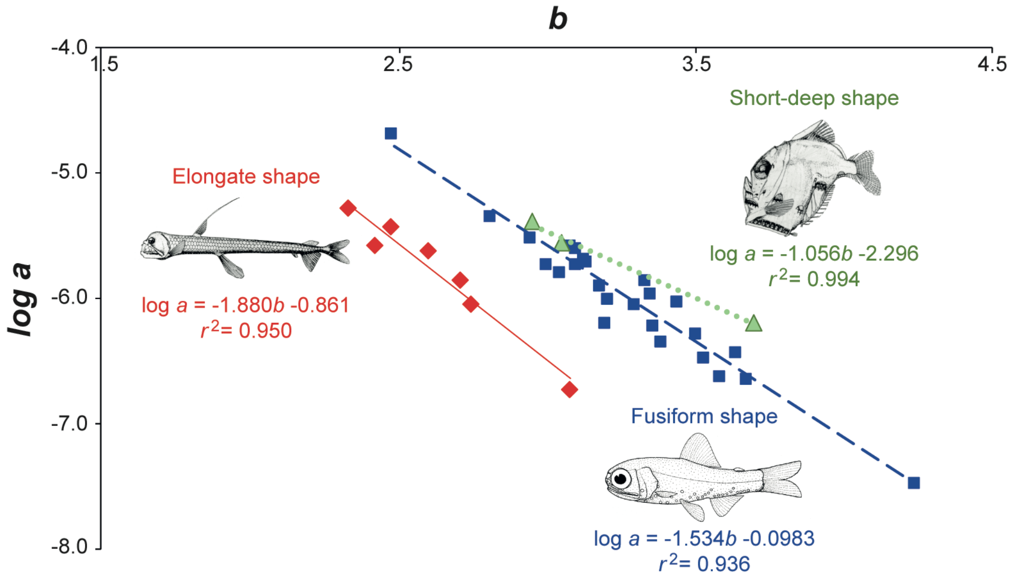
Equatorial
4
3
2
1
Oligotrophic
Brazil
ATLANTIC OCEAN



b
1.5
2.5
3.5
4.5
-4.0
-5.0
-6.0
-7.0
-8.0
log a
Short-deep shape
log a = -1.056b -2.296
r2= 0.994
Elongate shape
log a = -1.880b -0.861
r2= 0.950
Fusiform shape
log a = -1.534b -0.0983
r2= 0.936

TABLE 1 List of mesoplegic fishes from equatorial and tropical Atlantic waters analyzed in the present study. Region indicates the sampling origin according to Olivar *et al*. (2017): CB, Cape Blanc; CI, Canary Islands; CV, Cape Verde; O, oligotrophic; E, equatorial. Taxa were ordered according to Nelson *et al*. (2016)

Order	Family	Genera	Species	Author	Region
Stomiiformes	Gonostomatidae	*Cyclothone*	*Cyclothone acclinidens*	Garman, 1899	CV, CB
			Cyclothone lívida	Brauer, 1902	CV, CB
			Cyclothone pallida	Brauer, 1902	CV, CB
			Cyclothone pseudopallida	Mukhacheva, 1964	CV
		Gonostoma	*Sigmops elongatus*	(Günther, 1878)	E, CV, CB, CI
	Phosichthyidae	*Vinciguerria*	*Vinciguerria nimbaria*	(Jordan & Williams, 1895)	CV, CB
	Sternoptychidae	*Argyropelecus*	*Argyropelecus sladeni*	Regan, 1908	E , CV, CB
		Polypnus	*Polyipnus polli*	Schultz, 1961	CV, CB
		Sternoptyx	*Sternoptyx diaphana*	Hermann, 1781	CV, CB
	Stomiidae	*Chauliodus*	*Chauliodus danae*	Regan & Trewavas, 1929	E, CV, CB
		Stomias	*Stomias boa boa*	(Risso, 1810)	CV
Myctophiformes	Myctophidae	*Benthosema*	*Benthosema glaciale*	(Reinhardt, 1837)	CB
			Benthosema suborbitale	(Gilbert, 1913)	CV, CI
		Bolinichthys	*Bolinichthys photothorax*	(Parr, 1928)	O, E, CV
		Ceratoscopelus	*Ceratoscopelus warmingii*	(Lütken, 1892)	O, E, CV
		Diaphus	*Diaphus brachycephalus*	Tåning, 1928	O, E , CV, CB
			Diaphus dumerilii	(Bleeker, 1856)	E
			Diaphus fragilis	Tåning, 1928	E
			Diaphus holti	Tåning, 1918	CV, CB
			Diaphus metopoclampus	(Cocco, 1829)	E, CI
			Diaphus mollis	Tåning, 1928	O, E, CV
			Diaphus problematicus	Parr, 1928	E
			Diaphus rafinesquii	(Cocco, 1838)	CB, CI
			Diaphus vanhoeffeni	(Brauer, 1906)	CV
		Hygophum	*Hygophum macrochir*	(Günther, 1864)	CB (30)
		Lampanyctus	*Lampanyctus alatus*	Goode & Bean, 1896	E , CV, CB, CI
			Lampanyctus nobilis	Tåning, 1928	O, E
			Lampanyctus pusillus	(Johnson, 1890)	E, CB, CI
		Lepidophanes	*Lepidophanes guentheri*	(Goode & Bean, 1896)	O, E, CV
		Lobianchia	*Lobianchia dofleini*	(Zugmayer, 1911)	CV, CB, CI
		Myctophum	*Myctophum affine*	(Lütken, 1892)	CV
			Myctophum nitidulum	Garman, 1899	CV, CI
			Myctophum punctatum	Rafinesque, 1810	CB
		Notolychnus	*Notolychnus valdiviae*	(Brauer, 1904)	E, CV
		Notoscopelus	*Notoscopelus bolini*	Nafpaktitis, 1975	CB
			Notoscopelus resplendens	(Richardson, 1845)	E, CV, CB, CI

TABLE 2 Length-weight parametres for mesopelagic species (ordered alphabetically) from the equatorial and tropical Atlantic waters. *a*, intercept; *a*+, positive allometry; *a*-, negative allometry; *b*, allometry coefficient (slope); *eDW*, eviscerate body dry weight; *i*, isometry; n, sample size; *SL*, standard length; r^2, coeficient of determination; 95% CL of *b*, confidence interval

Species	n	Range *SL* (mm)	Range *eDW* (g)	*a*	*b*	Inferior 95% CL of *b*	Superior 95% CL of *b*	r^2	Growth model
Argyropelecus sladeni	27	15 − 43	0.012 − 0.186	0.00000414	2.950	2.472	3.428	0.866	i
Benthosema glaciale	15	15 − 35	0.005 − 0.145	0.00000035	3.647	3.486	3.809	0.990	a+
Benthosema suborbitale	29	16 −33	0.012 − 0.103	0.00000198	3.135	2.868	3.401	0.955	i
Bolinichthys photothorax	6	21 −51	0.021 − 0.335	0.00000121	3.183	2.944	3.421	0.997	i
Ceratoscopelus warmingii	47	16 −64	0.006 − 0.796	0.00000032	3.537	3.443	3.631	0.992	a+
Chauliodus danae	43	25 − 212	0.023 − 3.519	0.00000139	2.710	2.554	2.867	0.968	a-
Cyclothone acclinidens	22	31 −46	0.005 − 0.051	0.00000524	2.337	1.849	2.825	0.768	a-
Cyclothone livida	32	23 − 37	0.007 − 0.030	0.00000372	2.477	2.011	2.941	0.798	a-
Cyclothone pallida	24	25 − 54	0.009 − 0.073	0.00000235	2.600	2.270	2.929	0.924	a-
Cyclothone pseudopallida	19	23 − 35	0.004 − 0.017	0.00000258	2.420	1.596	3.244	0.693	i
Diaphus brachycephalus	100	12 − 47	0.002 − 0.749	0.00000131	3.339	3.194	3.482	0.956	a+
Diaphus dumerilii	30	31 − 57	0.089 − 0.628	0.00000254	3.076	2.865	3.285	0.970	i
Diaphus fragilis	10	46 − 79	0.183 − 1.022	0.00000155	3.056	2.740	3.371	0.984	i
Diaphus holti	91	11 − 50	0.002 − 0.491	0.00000106	3.356	3.250	3.460	0.978	a+
Diaphus metopoclampus	10	19 − 40	0.009 − 0.182	0.00000022	3.684	3.219	4.147	0.977	a+
Diaphus mollis	30	29 − 55	0.073 − 0.571	0.00000247	3.093	2.912	3.272	0.979	i
Diaphus problematicus	9	45 − 72	0.223 − 0.787	0.00000437	2.820	2.441	3.199	0.978	i
Diaphus rafinesquii	125	11 − 70	0.004 − 1.425	0.00000242	3.107	3.042	3.170	0.987	a+
Diaphus vanhoeffeni	17	25 − 36	0.054 − 0.154	0.00001968	2.488	1.856	3.119	0.825	i
Hygophum macrochir	30	20 − 42	0.018 − 0.223	0.00000190	3.138	2.973	3.302	0.982	i
Lampanyctus alatus	142	16 − 57	0.006 − 0.362	0.00000023	3.594	3.492	3.696	0.972	a+
Lampanyctus nobilis	19	28 − 74	0.022 − 0.619	0.00000061	3.205	2.906	3.503	0.968	i
Lampanyctus pusillus	22	24 − 36	0.019 − 0.132	0.00000003	4.247	3.638	4.855	0.914	a+
Lepidophanes guentheri	35	19 − 61	0.008 − 0.521	0.00000043	3.391	3.181	3.601	0.970	a+
Lobianchia dofleini	30	13 − 30	0.006 − 0.118	0.00000090	3.448	3.081	3.813	0.930	a+
Myctophum affine	34	14 − 47	0.005 − 0.328	0.00000049	3.509	3.384	3.633	0.990	a+
Myctophum nitidulum	25	15 − 74	0.006 − 1.233	0.00000084	3.308	3.219	3.396	0.996	a+
Myctophum punctatum	28	16 − 69	0.007 − 1.068	0.00000057	3.363	3.252	3.472	0.993	a+
Notolychnus valdiviae	27	15 − 22	0.019 − 0.123	0.00000289	2.956	2.956	3.577	0.816	i
Notoscopelus bolini	11	21 − 28	0.015 − 0.040	0.00000092	3.212	2.664	3.760	0.951	i
Notoscopelus resplendens	20	20 − 70	0.016 − 1.085	0.00000179	3.111	2.941	3.280	0.988	i
Polyipnus polli	34	16 − 43	0.019 − 0.627	0.00000064	3.697	3.431	3.962	0.962	a+
Sternoptyx diaphana	29	9 − 41	0.002 − 0.334	0.00000277	3.054	2.879	3.228	0.978	i
Stomias boa boa	20	53 − 153	0.041 − 1.073	0.00000019	3.081	2.855	3.305	0.979	i
Sigmops elongatus	35	45 − 151	0.029 − 0.962	0.00000089	2.746	2.608	2.883	0.980	a-
Vinciguerria nimbaria	32	14 − 50	0.005 − 0.226	0.00000177	3.005	2.932	3.077	0.996	i

TABLE 3 Mean water content (and standard deviation, sd) expressed as % of eviscerated wet weight in mesopelagic fishes from the equatorial and tropical Atlantic waters

Species	**mean ± sd**
Notolychnus valdiviae	58.99 ± 19.97
Polyipnus polli	71.31 ± 2.95
Lampanyctus pusillus	73.50 ± 3.73
Benthosema glaciale	73.63 ± 3.59
Diaphus fragilis	74.67 ± 0.80
Diaphus vanhoeffeni	75.14 ± 1.29
Myctophum nitidulum	75.19 ± 2.04
Diaphus problematicus	75.34 ± 1.20
Lobianchia dofleini	75.70 ± 2.28
Myctophum affine	75.76 ± 2.00
Diaphus dumerilii	76.20 ± 1.67
Vinciguerria nimbaria	76.22 ± 1.47
Notoscopelus resplendens	76.49 ± 1.44
Lepidophanes guentheri	76.50 ± 2.79
Diaphus holti	76.58 ± 3.44
Diaphus brachycephalus	76.89 ± 1.71
Diaphus mollis	77.49 ± 1.34
Benthosema suborbitale	77.60 ± 1.47
Diaphus rafinesquii	77.69 ± 2.01
Argyropelecus sladeni	78.15 ± 2.01
Lampanyctus alatus	78.24 ± 2.97
Sternoptyx diaphana	78.51 ± 2.90
Diaphus metopoclampus	79.05 ± 2.86
Cyclothone pseudopallida	79.07 ± 2.93
Bolinichthys photothorax	79.37 ± 1.30
Myctophum punctatum	79.53 ± 2.18
Cyclothone livida	79.69 ± 2.02
Notoscopelus bolini	79.77 ± 1.13
Ceratoscopelus warmingii	79.84 ± 2.49
Hygophum macrochir	79.93 ± 1.51
Cyclothone pallida	80.66 ± 2.19
Cyclothone acclinidens	81.21 ± 2.37
Lampanyctus nobilis	81.54 ± 1.51
Chauliodus danae	82.65 ± 5.82
Sigmops elongatus	83.35 ± 2.42
Stomias boa boa	83.90 ± 1.64

TABLE 4 Statistical comparison of Relative Condition Factor (K_{rel}) between oceanographic regions of the study area (Olivar *et al*., 2017) for mesopelagic fish species from the equatorial and tropical Atlantic waters. CB, Cape Blanc; CI, Canary Islands; CV, Cape Verde; E, equatorial; *eWD*, eviscerated dry weight (mg) ; *LWR*, length-weight relationship; n, number of specimens; ns, non-significant; *KW*, Kruskal-Wallis test; O, oligotrophic; sd, standard deviation; *SL*, standard length (mm); U, Mann-Whitney U test

Species	Region	n	*SL* range	*eDW* range	*LWR* equation	r^2	K_{rel} *mean (sd)*	Statistical analysis: test	*df*	*P*
Chauliodus dane	E	12	40-176	0.024-1.758	log *eWD* = 2.867 log *SL* -6.182	0.993	0.936 (0.090)	*t*-test = -0.294	33	ns
	CV	23	49-176	0.047-3.520			0.948 (0.112)			
Ceratoscopelus warmingii	E	23	16-64	0.071-0.796	log *eWD* = 3.610 log *SL* -6.581	0.992	1.072 (0.185)	*U* = 129, z = -1.552		ns
	CV	16	36-64	0.105-0.768			0.999 (0.101)			
Diaphus brachycephalus	O	34	30-53	0.101-0.606	log *eWD* = 3.264 log *SL* -5.767	0.972	0.792 (0.067)	*t*-test = -6.817	84	< 0.0001
	E	53	16-53	0.015-0.750			0.902 (0.076)			
Diaphus mollis	E	12	34-52	0.134-0.572	log *eWD* = 3.182 log *SL* -5.748	0.985	0.914 (0.076)	*t*-test = 1.169	20	ns
	CV	10	29-54	0.074-0.566			0.877 (0.069)			
Diaphus rafinesquii	CB	90	30-70	0.101-1.425	log *eWD* = 3.079 log *SL* -5.573	0.984	1.120 (0.094)	*t*-test = 0.063*	47	ns
	CI	34	30-58	0.118-0.773			1.118 (0.125)			
Lepidophanes guentheri	O	16	19-44	0.008-0.137	log *eWD* = 3.479 log *SL* -6.513	0.984	0.998 (0.187)	*t*-test = -1.312	28	ns
	E	14	34-61	0.077-0.522			1.088 (0.186)			
Myctophum nitidulum	CV	10	15-74	0.101-0.238	log *eWD* = 3.308 log *SL* -6.074	0.984	1.070 (0.102)	*U* = 72, z =-0.166		ns
	CI	15	18-57	0.118-0.231			1.051 (0.115)			
Vinciguerria nimbaria	CV	17	37-50	0.101-0.238	log *eWD* = 3.005 log *SL* -5.752	0.996	0.891 (0.083)	*t*-test = 0.088	30	ns
	CB	15	14-20	0.118-0.231			0.888 (0.083)			
								Post-hoc test after *KW*: CV	**CB**	**CI**
Lampanyctus alatus	E	22	27-48	0.027-0.217	log *eWD* = 3.594 log *SL* -6.648	0.972	1.067 (0.151)	ns	0.024	0.002
	CV	69	16-57	0.006-0.358			1.103 (0.152)		ns	0.004
	CB	25	34-51	0.072-0.363			1.195 (0.149)			ns
	CI	26	39-53	0.150-0.347			1.234 (0.171)			

**t-test for unequal variance*

TABLE S1 Length-weight parametres for mesopelagic species (ordered alphabetically) from the equatorial and tropical Atlantic waters. *a*, intercept; *a*+, positive allometry; *a*-, negative allometry; *b*, allometry coefficient (slope); *WW*, whole body wet weight; *i*, isometry; n, sample size; *SL*, standard length; r^2, correlation of determination; 95% CL of *b*, confidence interval

Species	n	Range *SL* (mm)	Range *WW* (g)	*a*	*b*	Inferior 95% CL of *b*	Superior 95% CL of *b*	r^2	Growth model
Argyropelecus sladeni	27	15 − 43	0.061 − 1.054	0.00000925	3.223	2.692	3.753	0.862	i
Benthosema glaciale	15	15 − 35	0.034 − 0.597	0.00000539	3.251	3.100	3.400	0.989	a+
Benthosema suborbitale	29	16 −33	0.069 − 0.527	0.00001615	2.982	2.592	3.371	0.943	i
Bolinichthys photothorax	6	21 −51	0.126 − 1.625	0.00001123	3.022	2.607	3.435	0.990	i
Ceratoscopelus warmingii	47	16 −64	0.038 − 3.865	0.00000442	3.284	3.195	3.371	0.992	a+
Chauliodus danae	43	25 − 212	0.062 − 29.083	0.00000267	2.976	2.868	3.083	0.987	i
Cyclothone acclinidens	22	31 −46	0.039 − 0.340	0.00004436	2.243	1.779	2.705	0.772	a-
Cyclothone livida	32	23 −37	0.040 − 0.195	0.00000599	2.846	2.340	3.351	0.815	i
Cyclothone pallida	24	25 − 54	0.051 − 0.434	0.00001276	2.616	2.210	3.020	0.891	i
Cyclothone pseudopallida	19	23 − 35	0.030 − 0.087	0.00005320	2.016	1.356	2.675	0.710	a-
Diaphus brachycephalus	100	12 − 47	0.014 − 3.557	0.00000906	3.243	3.123	3.362	0.967	a+
Diaphus dumerilii	30	31 − 57	0.423 − 2.681	0.00001689	2.981	2.763	3.199	0.966	i
Diaphus fragilis	10	46 − 79	0.871 − 4.415	0.00000971	2.976	2.798	3.152	0.995	i
Diaphus holti	91	11 − 50	0.020 − 2.367	0.00001677	3.006	2.887	3.124	0.966	i
Diaphus metopoclampus	10	19 − 40	0.066 − 0.943	0.00000398	3.353	2.914	3.791	0.975	i
Diaphus mollis	30	29 − 55	0.378 − 2.883	0.00001912	2.972	2.814	3.129	0.982	i
Diaphus problematicus	9	45 − 72	0.971 − 3.568	0.00001890	2.834	2.498	3.168	0.983	i
Diaphus rafinesquii	125	11 − 70	0.027 − 6.080	0.00003096	2.850	2.788	2.913	0.985	a-
Diaphus vanhoeffeni	17	25 − 36	0.265 − 0.691	0.00007869	2.530	2.088	2.972	0.908	a-
Hygophum macrochir	30	20 − 42	0.115 − 1.192	0.00002150	2.926	2.772	3.079	0.982	i
Lampanyctus alatus	142	16 − 57	0.047 − 1.795	0.00000488	3.199	3.106	3.290	0.971	a+
Lampanyctus nobilis	19	28 − 74	0.150 − 3.349	0.00000431	3.167	2.945	3.388	0.982	i
Lampanyctus pusillus	22	24 − 36	0.085 − 0.517	0.00000136	3.573	3.063	4.081	0.915	a+
Lepidophanes guentheri	35	19 − 61	0.056 − 2.564	0.00000642	3.108	2.932	3.282	0.975	i
Lobianchia dofleini	30	13 − 30	0.036 − 0.508	0.00001128	3.130	2.811	3.449	0.935	i
Myctophum affine	34	14 − 47	0.025 − 1.910	0.00000371	3.375	3.109	3.640	0.955	a+
Myctophum nitidulum	25	15 − 74	0.025 − 5.943	0.00000350	3.334	3.209	3.458	0.993	a+
Myctophum punctatum	28	16 − 69	0.042 − 4.582	0.00000545	3.221	3.131	3.311	0.995	a+
Notolychnus valdiviae	27	15 − 22	0.019 − 0.123	0.00000181	3.484	2.342	3.859	0.410	i
Notoscopelus bolini	11	21 − 28	0.085 − 0.221	0.00000719	3.101	3.484	1.720	0.905	i
Notoscopelus resplendens	20	20 − 70	0.065 − 4.832	0.00000837	3.108	2.894	3.320	0.981	i
Polyipnus polli	34	16 − 43	0.072 − 2.313	0.00000227	3.723	3.463	3.982	0.964	a+
Sternoptyx diaphana	29	9 − 41	0.014 − 1.861	0.00001472	3.104	2.900	3.308	0.973	i
Stomias boa boa	20	53 − 153	0.330 − 8.212	0.00000158	3.042	2.781	3.302	0.971	i
Sigmops elongatus	35	45 − 151	0.165 − 7.879	0.00000075	3.205	3.021	3.387	0.975	a+
Vinciguerria nimbaria	32	14 − 50	0.027 − 1.339	0.00000416	3.245	3.156	3.333	0.995	a+

TABLE S2 Length-weight parametres for mesopelagic species (ordered alphabetically) from the equatorial and tropical Atlantic waters. *a*, intercept; *a*+, positive allometry; *a*-, negative allometry; *b*, allometry coefficient (slope); *WW*, eviscerate body wet weight; *i*, isometry; n, sample size; *SL*, standard length; r^2, correlation of determination; 95% CL of *b*, confidence interval

Species	n	Range *SL* (mm)	Range *eWW* (g)	*a*	*b*	Inferior 95% CL of *b*	Superior 95% CL of *b*	r^2	Growth model
Argyropelecus sladeni	27	15 − 43	0.053 − 0.910	0.00000844	3.208	2.681	3.735	0.863	i
Benthosema glaciale	15	15 − 35	0.027 − 0.528	0.00000367	3.323	3.179	3.467	0.991	a+
Benthosema suborbitale	29	16 −33	0.060 − 0.478	0.00001402	2.993	2.584	3.401	0.943	i
Bolinichthys photothorax	6	21 −51	0.116 − 1.520	0.00000994	3.032	2.611	3.452	0.990	i
Ceratoscopelus warmingii	47	16 −64	0.033 − 3.368	0.00000364	3.303	3.214	3.391	0.992	a+
Chauliodus danae	43	25 − 212	0.059 − 22.652	0.00000266	2.957	2.855	3.059	0.988	i
Cyclothone acclinidens	22	31 −46	0.033 − 0.274	0.00004776	2.183	1.738	2.635	0.774	a-
Cyclothone livida	32	23 −37	0.039 − 0.146	0.00001491	2.538	2.032	3.045	0.777	i
Cyclothone pallida	24	25 − 54	0.047 − 0.380	0.00001526	2.540	2.135	2.944	0.885	a-
Cyclothone pseudopallida	19	23 − 35	0.027 − 0.083	0.00005324	1.986	1.178	2.794	0.613	a-
Diaphus brachycephalus	100	12 − 47	0.011 − 3.175	0.00000692	3.285	3.164	3.406	0.967	a+
Diaphus dumerilii	30	31 − 57	0.387 − 2.399	0.00001871	2.928	2.716	3.140	0.966	i
Diaphus fragilis	10	46 − 79	0.748 − 3.857	0.00000711	3.019	2.799	3.239	0.992	i
Diaphus holti	91	11 − 50	0.012 − 2.102	0.00000965	3.134	3.002	3.265	0.962	a+
Diaphus metopoclampus	10	19 − 40	0.064 − 0.802	0.00000330	3.349	2.979	3.718	0.982	i
Diaphus mollis	30	29 − 55	0.358 − 2.678	0.00001476	3.016	2.857	3.175	0.983	i
Diaphus problematicus	9	45 − 72	0.869 − 3.234	0.00001349	2.888	2.473	3.304	0.975	i
Diaphus rafinesquii	125	11 − 70	0.026 − 5.829	0.00002696	2.864	2.802	2.925	0.986	a-
Diaphus vanhoeffeni	17	25 − 36	0.248 − 0.584	0.00018969	2.238	1.740	2.735	0.860	a-
Hygophum macrochir	30	20 − 42	0.097 − 1.047	0.00001658	2.964	2.806	3.122	0.981	i
Lampanyctus alatus	142	16 − 57	0.040 − 1.720	0.00000418	3.214	3.121	3.306	0.971	a+
Lampanyctus nobilis	19	28 − 74	0.128 − 3.097	0.00000311	3.224	2.965	3.483	0.976	i
Lampanyctus pusillus	22	24 − 36	0.079 − 0.448	0.00000230	3.389	2.916	3.861	0.918	i
Lepidophanes guentheri	35	19 − 61	0.025 − 2.331	0.00000156	3.443	3.212	3.674	0.965	a+
Lobianchia dofleini	30	13 − 30	0.030 − 0.464	0.00000849	3.184	2.855	3.512	0.934	i
Myctophum affine	34	14 − 47	0.021 − 1.491	0.00000254	3.440	3.291	3.589	0.986	a+
Myctophum nitidulum	25	15 − 74	0.021 − 5.137	0.00000243	3.400	3.281	3.518	0.994	a+
Myctophum punctatum	28	16 − 69	0.036 − 3.863	0.00000438	3.232	3.137	3.326	0.995	a+
Notolychnus valdiviae	27	15 − 22	0.019 − 0.123	0.00000278	3.303	2.498	3.759	0.424	i
Notoscopelus bolini	11	21 − 28	0.077 − 0.195	0.00000594	3.129	3.302	1.587	0.933	i
Notoscopelus resplendens	20	20 − 70	0.060 − 4.427	0.00000756	3.114	2.908	3.320	0.983	i
Polyipnus polli	34	16 − 43	0.060 − 2.070	0.00000207	3.719	3.453	3.985	0.962	a+
Sternoptyx diaphana	29	9 − 41	0.009 − 1.604	0.00000729	3.236	3.038	3.434	0.977	a+
Stomias boa boa	20	53 − 153	0.312 − 7.306	0.00000159	3.013	2.739	3.292	0.967	i
Sigmops elongatus	35	45 − 151	0.147 − 7.149	0.00000064	3.220	3.064	3.376	0.982	a+
Vinciguerria nimbaria	32	14 − 50	0.023 − 0.964	0.00000594	3.073	2.989	3.158	0.995	i